DAILY BUDGETS OF PHOTOSYNTHETICALLY FIXED CARBON IN SYMBIOTIC ZOANTHIDS

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ABSTRACT

We tested the hypothesis that some zoanthids are able to meet a portion of their daily respiratory carbon requirement with photosynthetic carbon from symbiotic algal cells (= zooxanthellae). A daily budget was constructed for carbon (C) photosynthetically fixed by zooxanthellae of the Bermuda zoanthids *Zoanthus sociatus* and *Palythoa variabilis.*

Zooxanthellae have an average net photosynthetic C fixation of 7.48 and 15.56 $\mu gC \cdot polyp^{-1} \cdot day^{-1}$ for *Z. sociatus* and *P. variabilis* respectively. The C-specific growth rate (μ_c) was $0.215 \cdot day^{-1}$ for *Z. sociatus* and $0.152 \cdot day^{-1}$ for *P. variabilis.* The specific growth rate (μ) of zooxanthellae in the zoanthids was measured to be 0.011 and $0.017 \cdot day^{-1}$ for *Z. sociatus* and *P. variabilis* zooxanthellae respectively. *Z. sociatus* zooxanthellae translocated 95.1% of the C assimilated in photosynthesis, while *P. variabilis* zooxanthellae translocated 88.8% of their fixed C. As the animal tissue of a polyp of *Z. sociatus* required 14.75 $\mu gC \cdot day^{-1}$ for respiration, and one of *P. variabilis* required 105.54 $\mu gC \cdot day^{-1}$, the contribution of zooxanthellae to animal respiration (CZAR) was 48.2% for *Z. sociatus* and 13.1% for *P. variabilis.*

INTRODUCTION

Zoanthids (Cnidaria:Zoanthidea) are conspicuous and abundant members of shallow intertidal reef flat communities where scleractinian coral growth is not extensive (Sebens, 1982). Zoanthids contain dense populations of symbiotic algae (=zooxanthellae) which can fix carbon and translocate photosynthetic products to the animal host (Von Holt and Von Holt, 1968; Trench, 1974). Sebens (1977) has recently described the natural diet of the zoanthids *Zoanthus sociatus* and *Palythoa variabilis* at study sites in Panama and Brazil. Although the species exist in close proximity to each other, *P. variabilis* fed extensively on demersal zooplankton while *Z. sociatus* fed sparingly on small detrital particles. Sebens (1977) also demonstrated that although *Z. sociatus* lost weight when starved, significantly less weight was lost when starved in light sufficient for photosynthesis by symbiotic zooxanthellae. Because *Z. sociatus* fed on fewer, smaller food items than *P. variabilis,* Sebens (1977) conjectured that *Z. sociatus* polyps acquired a larger proportion of their daily carbon requirement from zooxanthellae than did *P. variabilis* polyps.

Using a new technique for analysis of daily C budgets in symbiotic cnidarians (Muscatine *et al.,* 1983; Muscatine *et al.,* 1984) it is now possible to obtain accurate estimates of at least four parameters associated with daily flux of photosynthetically fixed carbon: (1) the total daily net C fixed by zooxanthellae, (2) the amount of C used in growth of zooxanthellae, (3) the amount translocated to the animal, (4) and the contribution of translocated C to animal respiration.

This technique has been applied to symbiotic corals and has revealed that up to 97% of the carbon fixed in photosynthesis is translocated to the animal where it can potentially satisfy not only 100% of the animal daily requirement for respiration, but also a fraction of the carbon required for growth (Muscatine *et al.,* 1984).

In this paper we analyze the daily budget of photosynthetically fixed carbon in the zoanthids *P. variabilis* and *Z. sociatus* from shallow waters of Bermuda. We quantitatively assess the importance of photosynthetically fixed carbon to these animals, and compare our findings to previous work on zoanthid nutrition.

MATERIALS AND METHODS

Collection and maintenance of animals

Zoanthus sociatus and *Palythoa variabilis* were collected from Hungry Bay, Paget Parish, Bermuda at depths ranging from 0–0.3 m. The larger *P. variabilis* (2–4 cm high; 0.5–1.5 cm wide) were scattered among the polyps of the much smaller (0.5–1.5 cm high; 0.2–0.6 cm wide) and more abundant *Z. sociatus*. Small rocks with attached zoanthids were dislodged and transported in covered collecting buckets to the laboratory. Zoanthids were maintained in a 200 l plexiglass sea water tank (water flow rate = 2.4 l $\cdot$ min^{-1}) under natural sunlight outdoors. All animals were kept for a day in the tank and used in experiments within four days. To determine if maintenance conditions were adequate, the behavior of zoanthids in the tank was regularly monitored. The number of polyps fully or partially open per 1000 animals was counted for each species at 1–2 hour intervals over 24 hours.

Standing stock of zooxanthellae cell carbon (C')

Sixty-five randomly selected polyps of *Z. sociatus* were individually homogenized in a Waring blender equipped with a micro-attachment. Twelve randomly selected *P. variabilis* polyps were similarly treated. The homogenates were centrifuged at low speed and the resulting algal pellet resuspended in sea water. Numbers of zooxanthellae in the pellet were counted from samples using a Spencer Bright-Line haemacytometer. The diameter of 500 freshly isolated zooxanthellae was determined with an ocular micrometer and used to calculate average cell carbon according to Strathmann (1967). Standing stock of algae is expressed as number of cells per polyp, or as algal carbon per polyp.

Photosynthesis versus irradiance curves of zooxanthellae

Total C fixed daily was determined from measurements of photosynthetic rates at various irradiances using the ^{14}C technique (Strickland and Parsons, 1977). Individual zoanthid polyps were clipped from colonies and allowed two days to heal before use. Healthy polyps were placed in conical centrifuge tubes in 1 ml of Millipore filtered (0.45 μm) seawater. Tubes were wrapped with plastic neutral-density screens and placed in front of a bank of Cool-White fluorescent lights to obtain a range of irradiances from 0–360 μ Einsteins $\cdot$ m^{-2} $\cdot$ s^{-1}. Six ml of a stock solution of NaH^{14}CO$_3$ in filtered sea water was added to each tube so that the total dose was 1 μCi per tube. Three 0.1 ml samples were taken immediately for measurement of added activity. Polyps were incubated 1 hour at 27–28°C, followed by addition of 0.5 ml of 40% formalin to each tube and refrigeration at 5°C before further processing. Subsequently each polyp was individually homogenized and the zooxanthellae quantitatively isolated as

before. The animal homogenate was adjusted to 12 ml and a 0.4 ml aliquot was placed in a scintillation vial, acidified with 1 N HCl, and evaporated to dryness at low heat on a Waring hot plate to remove unused $^{14}CO_2$. Ten ml of Aquasol was added to the dried sample and radioactivity was measured in a Beckman LS-100C liquid scintillation counter using a ^{14}C wide window isoset.

Algal pellets were resuspended in 1 ml of Millipore filtered (0.45 μ) sea water. A 0.5 ml aliquot was filtered, rinsed, acidified, and counted in 10 ml Aquasol. The remainder of the algal suspension was saved for haemacytometer counts.

Scintillation counts were quench corrected and disintegrations per minute (dpm) in the animal and algal fractions were summed to obtain total dpm per polyp. Total weight of carbon fixed was calculated (Strickland and Parsons, 1977), corrected for dark fixation, and expressed as net carbon fixed. Data were normalized to the number of zooxanthellae counted in individual animals and regressed against irradiance. Photosynthetic capacity (P_{max}) was calculated as the average of the total carbon fixed in all experiments at or above saturation.

Total daily net photosynthesis of zooxanthellae was calculated from the hourly rate of photosynthesis at saturation multiplied by the number of hours each zoanthid was at saturating irradiance.

Natural ambient irradiance was measured on 8 September 1983 with a LiCor 185 light meter equipped with a quantum sensor. The sensor was taped to an unshaded horizontal surface and readings were taken at intervals from 6:15 AM to 8:00 PM.

Specific growth rate of zooxanthellae

The carbon specific growth rate (μ_c) was calculated from:

$$\mu_c = \frac{1}{C'} \cdot \frac{\Delta C}{\Delta t}$$

where C' is the standing stock of algal carbon, and $\Delta C/\Delta t$ is the increment of C added per day (= net carbon fixed per day).

Cell specific growth rate (μ) was estimated by the method of Wilkerson *et al.* (1983), using zooxanthellae harvested from each zoanthid species at 2 hour intervals for 24 hours. The algal pellet was preserved in 4% formalin in sea water and the number of cells in cytokinesis (*i.e.*, a "doublet" with a cell wall plate) was counted in each of 10 fields of 200 zooxanthellae viewed at 430×. The specific growth rate (μ) of zooxanthellae was calculated from:

$$\mu = \frac{1}{t_d} \ln(1 + f)$$

where f is the average mitotic index, and t_d is the duration of mitosis, taken here as 0.46 days (McDuff and Chisholm, 1983; Wilkerson *et al.,* 1983).

Translocation of carbon from zooxanthellae to host

Fixed carbon translocated daily from zooxanthellae was estimated by the growth rate method (Muscatine *et al.,* 1983) such that $\mu_c - \mu = \mu_T$ where μ_T is the specific translocation rate and T is the percent total daily translocation, such that:

$$T = \frac{\mu_c - \mu}{\mu_c} \times 100$$

Respiration

Respiration of the intact plant-animal association was measured by placing freshly collected polyps of each species separately in 5-l Niskin sampling bottles (General Oceanics Model 1010) filled with sea water from the running sea water system. Bottles were incubated for 12 hours in darkness at 27–28°C, then water from the Niskin bottles was run into replicate BOD bottles. Dissolved oxygen was measured in the water before and after incubation using the Winkler technique (Strickland and Parsons, 1977).

To estimate the respiration of the animal component we assumed that the ratio of plant to animal respiration was proportional to their protein biomass ratio (Muscatine *et al.*, 1981). The protein content of freshly separated plant and animal tissues in each polyp was measured after incubation using the method of Lowry *et al.* (1951) with bovine serum albumin as a standard.

The daily contribution of zooxanthellae to animal respiration (CZAR)

Since daily translocation represents the carbon supply and daily animal respiration the carbon demand, CZAR was calculated from:

$$CZAR = \frac{\text{Net C fixed daily}}{R_a} \cdot T$$

where R_a = total daily animal respiratory requirement for carbon (Muscatine *et al.*, 1983).

<div align="center">RESULTS</div>

Expansion and contraction of polyps

To determine if maintenance and incubation conditions were adequate to sustain normal behavior patterns, we compared the pattern of expansion and contraction of polyps of both zoanthid species. Figure 1 shows that as many as 75% of the polyps of *P. variabilis* were fully or partially expanded in darkness, while only 1–4% of the polyps were expanded in full sunlight. In contrast, those of *Z. sociatus* showed an irregular pattern of expansion and contraction, with groups of polyps showing similar behavior. *Z. sociatus* polyps did not show a marked response to light, but contracted rapidly in response to wind-driven water disturbances.

These patterns of expansion and contraction of zoanthids in the holding tank were similar to those seen by Sebens (1977) for these species in the field, and persisted until at least four days after collection, suggesting that maintenance conditions did not perturb normal expansion and contraction behavior.

Standing stock of zooxanthellae

Table I shows that *Z. sociatus* polyps harbor an average of 1.11×10^6 zooxanthellae, while polyps of the larger *P. variabilis* contain 52% more zooxanthellae. Since zooxanthellae were isolated collectively from a group of zoanthids, the range of variation in zooxanthellae per polyp is unknown.

Zooxanthellae isolated from *P. variabilis* were significantly larger (2-sample *t*-test, $P < 0.0005$) and had more than twice the volume and twice the cell carbon than zooxanthellae from *Z. sociatus*. Polyps of the larger *P. variabilis* contained almost three times as much algal carbon as those of *Z. sociatus*.
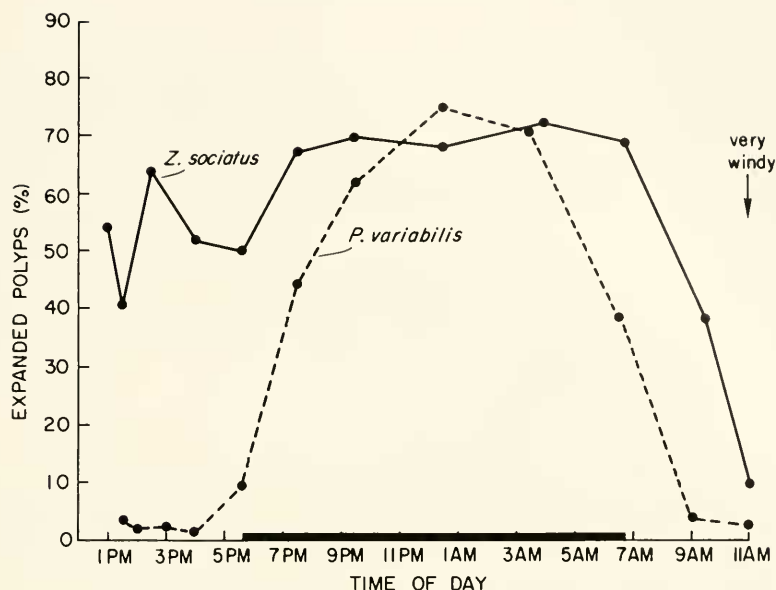
FIGURE 1. The diel pattern of polyp expansion of zoanthids in the outdoor aquarium. Note similarity to behavior in the field reported by Sebens (1977). Arrow indicates first observation time affected by a gusting wind which began shortly after 9 AM.

Photosynthesis/irradiance curves for intact zoanthids

Figure 2 shows the photosynthesis/irradiance (P/I) curves derived for both zoanthid species. The P/I curve for *Z. sociatus* is linear up to at least 360 μ Einsteins $\cdot$ m^{-2} $\cdot$ s^{-1} and may extend beyond this point before saturating. Consequently, our estimate for P_{max} may well be conservative. During the $^{14}CO_2$ incubation these polyps randomly expanded and contracted as did their counterparts in the holding tank. Zooxanthellae were therefore exposed to irradiance that was attenuated by an animal body wall of variable thickness. This may account for the lower correlation coefficient.

The P/I curve for *P. variabilis* is linear up to about 180 μ Einsteins $\cdot$ m^{-2} $\cdot$ s^{-1}. There was relatively little variation in photosynthesis at a given irradiance. During the $^{14}CO_2$ incubation these zoanthids were contracted and showed little change in posture. Thus the zooxanthellae in *P. variabilis* may have received a more constant light flux penetrating the body wall than in *Z. sociatus* and the rate of photosynthesis would not be affected by changes in body wall thickness.

TABLE I

Biomass parameters of zoanthids

Zoanthid	Zooxanthellae cells $\cdot$ polyp^{-1} ($\times 10^6$)	Zooxanthellae diameter (μm $\pm$ S.D.)	Zooxanthellae cell volume (μm^3)	Zooxanthellae carbon $\cdot$ cell^{-1} (pg)	Zooxanthellae C $\cdot$ polyp^{-1} (μg)
Z. sociatus	1.11	7.025 $\pm$ 0.79	181.5	31.35	34.80
P. variabilis	1.69	9.050 $\pm$ 3.42	388.2	60.56	102.35

Daily net carbon fixed

Figure 3 shows the measured irradiance at the Bermuda Biological Station on 8 September 1983, a clear cloudless day. This curve of light available for photosynthesis on a "representative day" was used in conjunction with the P/I curves to calculate the total daily increment of carbon fixed by zooxanthellae photosynthesis. Our estimate of absolute values of net daily photosynthesis is strictly valid only for the day on which the diel irradiance curve was recorded, but it reflects the potential for any day. The method also assumes that photosynthesis at dawn and dusk, at levels below P_{max}, does not significantly contribute to total diel C fixation.

Table II shows net hourly C fixation at P_{max} normalized to 10^6 zooxanthellae and to an average polyp of each species. The data show that *P. variabilis* fixed twice as much carbon per polyp per day as *Z. sociatus*.

Cell specific growth rate of zooxanthellae

Figure 4 shows the average number of dividing zooxanthellae per 200 zooxanthellae examined for each host. Zooxanthellae in both hosts were characterized by a low specific growth rate with an average of 0.63% algal cells in division. Zooxanthellae of *Z. sociatus* showed no phasing of cell division, but *P. variabilis* zooxanthellae showed slight phasing of cell division beginning at 11 PM. The number of dividing cells among *P. variabilis* zooxanthellae is significantly higher (two sample *t*-test; *P* < 0.01) than for *Z. sociatus* zooxanthellae in several of the night time samples. The growth rate of *Z. sociatus* zooxanthellae was 0.0105 day^{-1} (doubling time = 66 days) and for *P. variabilis* μ = 0.0170 day^{-1} (doubling time = 41 days) (Table III).
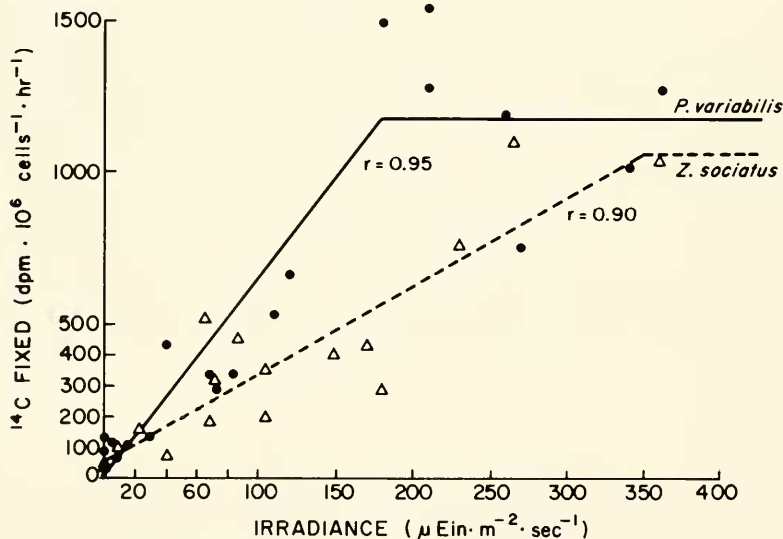

FIGURE 2. The photosynthetic carbon-14 fixation of intact zoanthids *versus* irradiance. The lower linear portion of each curve was fitted by linear regression with data points added in order of increasing irradiance. Correlation coefficients (r) were calculated for each new data point and the point at which the r value began to decline progressively was taken as the last point on the linear portion of the curve. Photosynthesis at saturation (P_{max}) was calculated as the average of the remaining points.
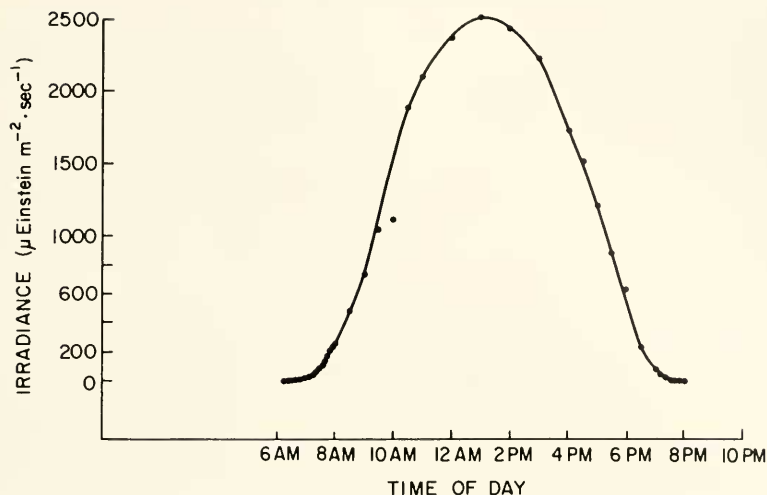
FIGURE 3.   Diel irradiance at the Bermuda Biological Station on 8 September 1983, a clear cloudless day.

Translocation

The fraction of C translocated from zooxanthellae is shown in Table III, and the amount of C translocated is calculated from the product of net C fixed daily (Table II) and the percent translocation (Table III). Carbon translocated is substantial in both cases, but greater in *Z. sociatus*.

Respiration

From data on polyp respiration and protein biomass ratios (Table IV) we calculated the average daily animal respiration rate per polyp (Table V). Although the rate of respiration by the larger *P. variabilis* polyps is more than six times that of *Z. sociatus*, their specific metabolic rates are similar (Table V).

Contribution of zooxanthellae to animal respiration (CZAR)

From data on weight of C translocated, and weight of C required for animal respiration we calculated CZAR. CZAR is nearly 50% in *Z. sociatus* polyps but only 13% in *P. variabilis* polyps (Table V).

TABLE II

Total carbon fixed daily by zooxanthellae

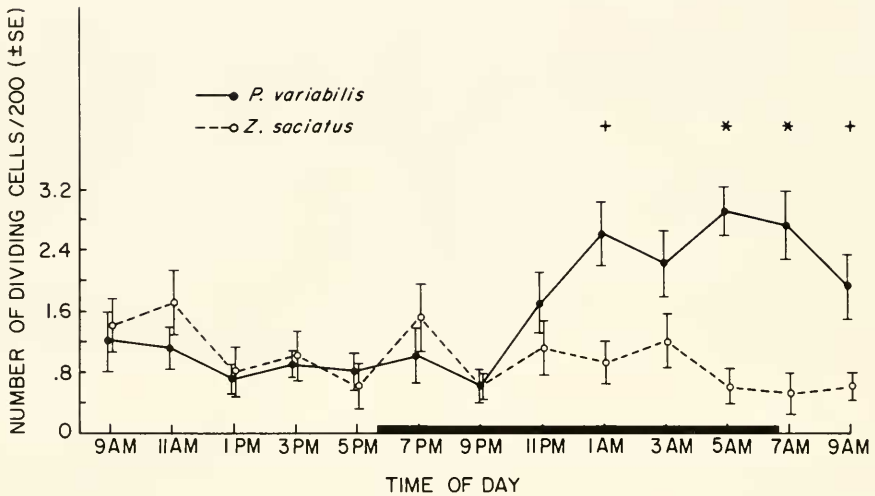| Zoanthid species	Saturating irradiance (μEin · $m^{-2} \cdot s^{-1}$)	Net hourly C fixation at P_{max}		Time at P_{max} (hours)	Net daily C fixation	
		(μg · 10^6 cells$^{-1} \cdot h^{-1}$)	(μg · polyp$^{-1} \cdot$ h^{-1})		(μg · 10^6 cells$^{-1} \cdot$ day^{-1})	(μg · polyp$^{-1} \cdot$ day^{-1})
Z. sociatus	360	0.65	0.72	10.3	6.74	7.48
P. variabilis	180	0.86	1.45	10.7	9.21	15.56

FIGURE 4. Diel variation in number of dividing cells per 200 zooxanthellae. Dividing cells are defined as paired cells or doublets with a division plate between nuclei. Points shown are the mean of 10 counts of cells ± SEM. Significant differences between zooxanthellae from the two zoanthid hosts are seen at several times; levels of significance are (+) $P < .05$ and (*) $P < .001$ (two-sample t-test).

DISCUSSION

The results of this investigation show that zooxanthellae of *P. variabilis* and *Z. sociatus* assimilate substantial amounts of carbon during photosynthesis. The surplus beyond that needed for zooxanthellae respiration and growth can be translocated to the zoanthid host and used to satisfy a portion of the daily animal respiratory requirement for carbon. Our data suggest that zooxanthellae of *Z. sociatus* may contribute 48.2% of the daily animal respiratory requirement for carbon, while zooxanthellae of *P. variabilis* can contribute only 13.1% We conclude that, in order to meet its daily C requirement for respiration, *P. variabilis* is dependent to a greater extent upon feeding than *Z. sociatus*. This conclusion supports that of Sebens (1977).

Both *Z. sociatus* and *P. variabilis* feed on minute particles suspended in the water column. *P. variabilis* obtains demersal zooplankton by tentacular feeding at night while *Z. sociatus* polyps are continuously expanded and feed on small detrital particles rather than whole zooplankton (Sebens, 1977). The greater dependence of *P. variabilis* on capture of demersal zooplankton is correlated with nocturnal polyp expansion behavior (Fig. 1), elongated tentacles, and a tall, columnar body (Koehl, 1977). *Z. sociatus,* which is less dependent upon zooplankton, expands irregularly (Fig. 1), and

TABLE III

Growth rates and translocation by zoanthid zooxanthellae

Zoanthid species	μ_c (day^{-1})	μ (day^{-1})	C translocated daily	
			(%)	(μg · polyp^{-1} · day^{-1})
Z. sociatus	0.215	0.011	95.11	7.11
P. variabilis	0.152	0.017	88.80	13.82

TABLE IV

Protein biomass ratios of zoanthids

Zoanthid species	Zooxanthellae protein $\cdot$ polyp^{-1} (mg)	Total protein $\cdot$ polyp^{-1} (mg)	Protein biomass ratio (animal:total protein)
Z. sociatus	0.388	2.268	0.829
P. variabilis	0.516	14.706	0.965

possesses short tentacles and a matting colony morphology which is less suitable for raptorial zooplankton capture (Porter, 1976; Koehl, 1977; Sebens, 1977). The amount of carbon derived from algal photosynthate thus bears an inverse relation to the dependence on heterotrophic C acquisition.

We note that the rates of translocation determined here by the growth rate method are the highest yet reported for symbiotic zoanthids. They are substantially higher than rates reported by Trench (1974) whose analysis was based on the *in vitro* ^{14}C method. These and other methods are critically reviewed in Muscatine *et al.* (1984).

Error in the estimate of P_{max} will substantially change the calculated value for the increment of carbon fixed per day. The P_{max} value for *P. variabilis* is the average of six data points and shows light saturation at irradiances higher than 180 μ Einstein $m^{-2} \cdot s^{-1}$. The P/I curve for *Z. sociatus* does not show a clearcut point at which light saturation begins and it is possible that zooxanthellae in this host were not saturated even at 360 μ Einstein $\cdot m^{-2} \cdot s^{-1}$. If this is true, then *Z. sociatus* zooxanthellae may be capable of fixation of a larger increment of carbon per day than our figures show, and CZAR for this host may be higher than 48.2%. CZAR varies directly with P_{max} such that, all other values being constant, CZAR will increase by 1% for every 1% increase in P_{max}.

The quantitative assessment of P_{max} is conservative because it was measured using a radiotracer technique. Although ^{14}C measurements of plant productivity often overestimate net C uptake (Peterson, 1980), Smith (1982) has pointed out that, in short-term experiments (*e.g.,* 30'–120'), ^{12}C bicarbonate/^{14}C-bicarbonate disequilibrium may result in underestimates of C release by more than 50%.

A major assumption of the carbon budget analysis is that the net carbon assimilated by algal photosynthesis is used only for algal growth or translocation to the host. Other carbon sinks may exist which are not incorporated into this analysis. If zooxanthellae are capable of intracellular storage of significant quantities of fixed carbon our estimate of daily carbon translocation will be high. Storage, however, should

TABLE V

Respiration and CZAR in zoanthids

Zoanthid species	Polyp respiratory rate (μg O$_2 \cdot$ day^{-1})	Animal respiratory rate (μg O$_2 \cdot$ day^{-1})	Animal specific metabolic rate (μg O$_2 \cdot$ mg protein$^{-1} \cdot$ day^{-1})	Animal C requirement[1] (μg)	C supplied / C required (%)
Z. sociatus	56.92	47.19	25.1	14.75	48.2
P. variabilis	350.00	337.75	23.8	105.54	13.0

[1] Respiratory quotient = 0.8.

produce a change in zooxanthellae volume which was not observed in our samples (Goto *et al.,* pers. commun.). If zoanthids are able to digest zooxanthellae, our estimate of CZAR may be too low.

Determination of the animal daily carbon requirement for respiration depends upon the assumption that the protein biomass ratio of algal and animal components is proportional to their respiration ratio (Muscatine *et al.,* 1981) (*i.e.,* that the specific metabolic rate of the algal and animal tissue is equal). This assumption is difficult to test in intact associations. It is noteworthy that the dark respiration rate of freshly isolated zooxanthellae of the coral *Stylophora pistillata* is nearly 8 times higher than the calculated respiration rate for algae *in situ* (McCloskey and Muscatine, 1984). Some insight may be gained from measurement of the respiratory rate of aposymbiotic hosts, but such hosts would not have translocated substrates to metabolize and therefore would not reflect conditions in the intact association.

A four-fold difference in CZAR exists between *Z. sociatus* and *P. variabilis.* This difference is correlated with a five-fold difference in biomass ratio. A correlation between CZAR and biomass ratio may be a general feature of coelenterate symbioses since it has been observed in several coral and anemone associations (G. Parker, pers. comm.). If a partially heterotrophic organism is to increase its reliance on autotrophic C, either the proportion of space allotted to algae must increase or the metabolic rate of the heterotroph must decrease. The specific metabolic rate of animal tissue in the two zoanthid species is equivalent (Table V), suggesting that *Z. sociatus* can rely more on autotrophic C acquisition because it has proportionally more autotrophic tissue. The protein biomass ratio of *Z. sociatus* is unusually low compared to the biomass ratios of 0.86–0.97 reported for other symbiotic cnidarians (Muscatine, 1980).

Although the work reported here provides evidence for potential quantitative benefit to zoanthids which maintain algal endosymbionts, it does not demonstrate that this potential is realized. When considered in conjunction with experiments demonstrating that zoanthid weight loss during starvation in the light is less extensive than weight loss in the dark (Sebens, 1977), we conclude that zoanthids derive substantial benefit from translocated algal photosynthate and that this benefit may vary in a species-specific manner.

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